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Biotope and biocenosis of cryoconite hole ecosystems on Ecology Glacier in the maritime Antarctic

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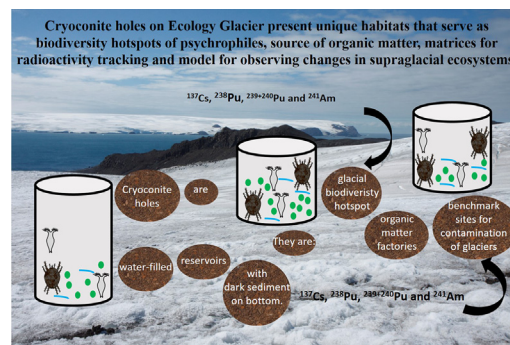
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HIGHLIGHTS

- 17 taxa of algae and cyanobacteria, 3 taxa of rotifers, and 1 of mite were found
- Cryoconite holes on Ecology Glacier were dominated by Bacillariophyceae
- In cryoconite holes, a suspension-feeding mite species was observed and identified first time
- Investigated artificial radionuclides included ^{137}Cs , ^{238}Pu , $^{239+240}\text{Pu}$ and ^{241}Am
- Cryoconite holes on Ecology Glacier present unique inland habitats for psychrophiles

GRAPHICAL ABSTRACT



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ABSTRACT

Despite recent great interest in glacier ecosystems in the continental Antarctic, little is known about their maritime counterparts. Our study presents descriptive data on cryoconite sediments and cryoconite holes on Ecology Glacier (King George Island) to accomplish three main objectives: (a) to identify main eukaryotic (algae, invertebrates) and prokaryotic (cyanobacteria) components of microbial communities; (b) to provide a "baseline" of community composition, organic matter and artificial contamination; and (c) to identify key abiotic factors that might be important in community assembly. Cryoconite holes were sampled along an altitudinal gradient of Ecology Glacier in January, mid Austral Summer 2017. Cryoconite holes located in lower altitude were deeper than those located in the middle and the highest altitude. Seventeen species of algae and cyanobacteria with biomass of 0.79 to 5.37 $\mu\text{g}/\text{cm}^3$ have been found in sediments. Dominant species were cyanobacterial *Pseudanabaena frigida* and Bacillariophyceae *Microcosta* sp. Biomass of Bacillariophyceae was significantly higher than that of Chlorophyta and Cyanobacteria. We found three species of rotifers (potentially two new to science) and for the

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Contamination of polar regions
Acari and freshwater Rotifera
Glacial ecosystems
Microbial communities

first time a glacier dwelling Acari (suspension feeder, *Nanorchestes nivialis*). Organic matter content ranged from 5.4% to 7.6%. Investigated artificial radionuclides included ^{137}Cs , ^{238}Pu , $^{239+240}\text{Pu}$ and ^{241}Am . ^{210}Pb seems to be related to organic matter content. Overall, cryoconite holes on Ecology Glacier present unique habitats that serve as biodiversity hotspots of psychrophiles, source of organic matter, matrices for radioactivity tracking and model for observing changes in supraglacial ecosystems in the maritime Antarctic.

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1. Introduction

For years glaciers have been considered as unproductive and mostly lifeless systems. Over the last two decades, a new view of glaciers as the coldest of Earth's biomes and biodiversity hotspots of psychrophiles has emerged (Anesio and Laybourn-Parry, 2012; Stibal et al., 2020). Glaciers' biological activity peaks during summers (Hodson et al., 2008; Anesio and Laybourn-Parry, 2012) when liquid water accumulates on the surface of glaciers (supraglacial zone) providing habitable space for microbial communities. Most of the organisms within those communities are unique and highly adapted to cope with extreme cold, frequent cycles of melting and freezing, flushing of nutrients, and high UV radiation (e.g., Hodson et al., 2008; Zawierucha et al., 2019; Samui et al., 2018). Through their activity, they can affect local carbon and iron budgets, and rates of ice melting (Anesio et al., 2009; Tedstone et al., 2017; Williamson et al., 2018).

The most biologically diverse, active, and productive glacial communities are those associated with cryoconite holes (Takeuchi et al., 2010; Stibal et al., 2015, 2020; Cook et al., 2015; Zawierucha et al., 2015). They form when supraglacial sediment (mineral debris deposited on the surface of ice by wind, water, and rockfall) along with microorganisms (e.g., bacteria, algae, and invertebrates) (Takeuchi et al., 2001a; Hodson et al., 2008; Cook et al., 2015) absorb more solar radiation than the surrounding ice and melt into the ice. Cryoconite holes are considered biodiversity hotspots, bioreactors producing organic matter, and potential sinks of heavy metals and other contaminants (Wharton et al., 1985; Stibal et al., 2010; Baccolo et al., 2017; Łokas et al., 2016, 2018, 2019; Zawierucha et al., 2018). Many species are associated exclusively with these unique glacial ecosystems (Dastyk et al., 2003; Edwards et al., 2013; Zawierucha et al., 2015, 2016a). Although the seedbank of cryoconite communities originates from habitats surrounding glaciers (e.g., soils, supraglacial gravel and streams) (Franzetti et al., 2017), they develop their own distinct signatures (Franzetti et al., 2017; Stibal et al., 2020; Zawierucha et al., 2016a). Even though studies on biological and ecological characteristics of glaciers have been conducted worldwide (Franzetti et al., 2017; Segawa et al., 2017; Stibal et al., 2015; Zawierucha et al., 2019) including Antarctica, the knowledge on glaciers in the Maritime Antarctica remains scarce. Despite the fact that Antarctica is the most extensive ice covered part of the world, its glacier ecosystems seem to be poorly known, with comprehensive studies conducted only on a few glaciers (Porazinska et al., 2004; Sommers et al., 2019; Stanish et al., 2013).

Antarctica is the only continent covered by 97% of ice and thus it constitutes the largest freshwater reservoir on Earth. Glaciers play an important role in Antarctic ecosystems as a source of water and nutrients for forefields in polar deserts (Bagshaw et al., 2013) but also as a source of nutrients for aquatic systems (Hodson et al., 2017). Despite a long history of studies on glacial ecosystems in Continental Antarctic, special attention has been given only to microbial diversity, its function, and cryoconite holes morphology and biochemistry mostly on McMurdo Dry Valley glaciers (Bagshaw et al., 2007, 2011, 2013; Fountain et al., 2004; Mueller et al., 2001; Porazinska et al., 2004; Sommers et al., 2019; Wharton et al. 1985), the knowledge on glacial ecosystems in the Maritime Antarctica remains scarce. Maritime Antarctica, especially the Antarctic Peninsula, is a transition zone, where climatic conditions vary between the north and more polar-influenced south. Therefore,

the Antarctic Peninsula is characterised by unique conditions including climate and isolation from human impact. Owing to its remote location, the Antarctic Peninsula has been already suggested as an area suitable for monitoring the effects of climate change (Braun & Gossmann, 2002) and air pollution (Artaxo et al., 1992). Given that cryosphere is one of the fastest changing biomes (Quayle et al., 2002; Robinson et al., 2003; Convey, 2013), physical and biological description of supraglacial habitats for developing a better understanding of glacial ecosystem functioning, their biodiversity, human impact and organic matter losses from ice to downstream ecosystems is urgent.

The present study lays out groundwork on cryoconite hole ecosystems of Ecology Glacier in Maritime Antarctica. Specifically, it identifies diversity and composition of microbial eukaryotes (algae, invertebrates) and prokaryotes, characterizes abiotic conditions, and describes the extent of biotic/abiotic interactions.

2. Material and methods

2.1. Study area

2.1.1. King George Island

King George Island (KGI) is located between 61°54'–62°16'S and 57°35'–59°02'W in the South Shetland archipelago (West Antarctica, Fig. 1). This island was formed on a crustal block with a thickness of 30–32 km separated from the Antarctic Peninsula (Birkenmajer et al., 1991). The KGI rocks (Igneous rock) are mainly rich in both calcium and alkali metals and there is a low abundance of trace elements. >90% of the land is covered by ice with the highest point being 650 m a.s.l. with the glacier equilibrium-line at about 100 m a.s.l. (Bintanja, 1995). The whole island is characterised by a typical maritime climate with low annual amplitudes of air temperature (2 °C), high humidity (82%) (Martianov and Rakusa-Suszczewski, 1989) as well as constant cloud cover (Rakusa-Suszczewski et al., 1993; Knap et al., 1996; Braun et al., 2001; Ferron et al., 2004). The average annual (1977–1998) sum of precipitation at the Arctowski station is 499.8 mm with two maxima in March and September (58.3 mm and 47.4 mm respectively), and two minima in August and December (28.2 mm and 34.7 mm respectively) (Marsz and Styszyńska, 2000).

2.1.2. Ecology Glacier

Ecology Glacier (62°11'S, 58°28'W) is located in the southern part of the KGI. The glacier is an outlet from the Warszawa Icefield flowing north-east. The central part of the front empties into the Suszczewski Cove of the Admiralty Bay while lateral parts of the lobe terminate on land forming marginal moraines. The surface area of the basin of Ecology Glacier is 5.21 km² (Pętllicki et al., 2017). Overall glacier mass balance is driven by both frontal and surface ablation, which over the last 40 years has been negative (Pętllicki et al., 2017). This reflects a concurrent climate warming trend of 0.19 °C per decade (Sobota et al., 2015; Kejna et al., 2012). Recently, observed positive net surface mass balance (Sobota et al., 2015), similar to other glaciers in the Antarctic Peninsula (Navarro et al., 2013; Oliva et al., 2017), may be explained by a regional cooling recorded in the last few years (Turner et al., 2016; Pętllicki et al., 2017). The temporal variation of climatic conditions is expressed in surface lowering rate since 1979, ranging from -1.7 m y^{-1} (1979–2001) to -0.5 m y^{-1} (2012–2016) (Pętllicki et al., 2017). The same pattern is

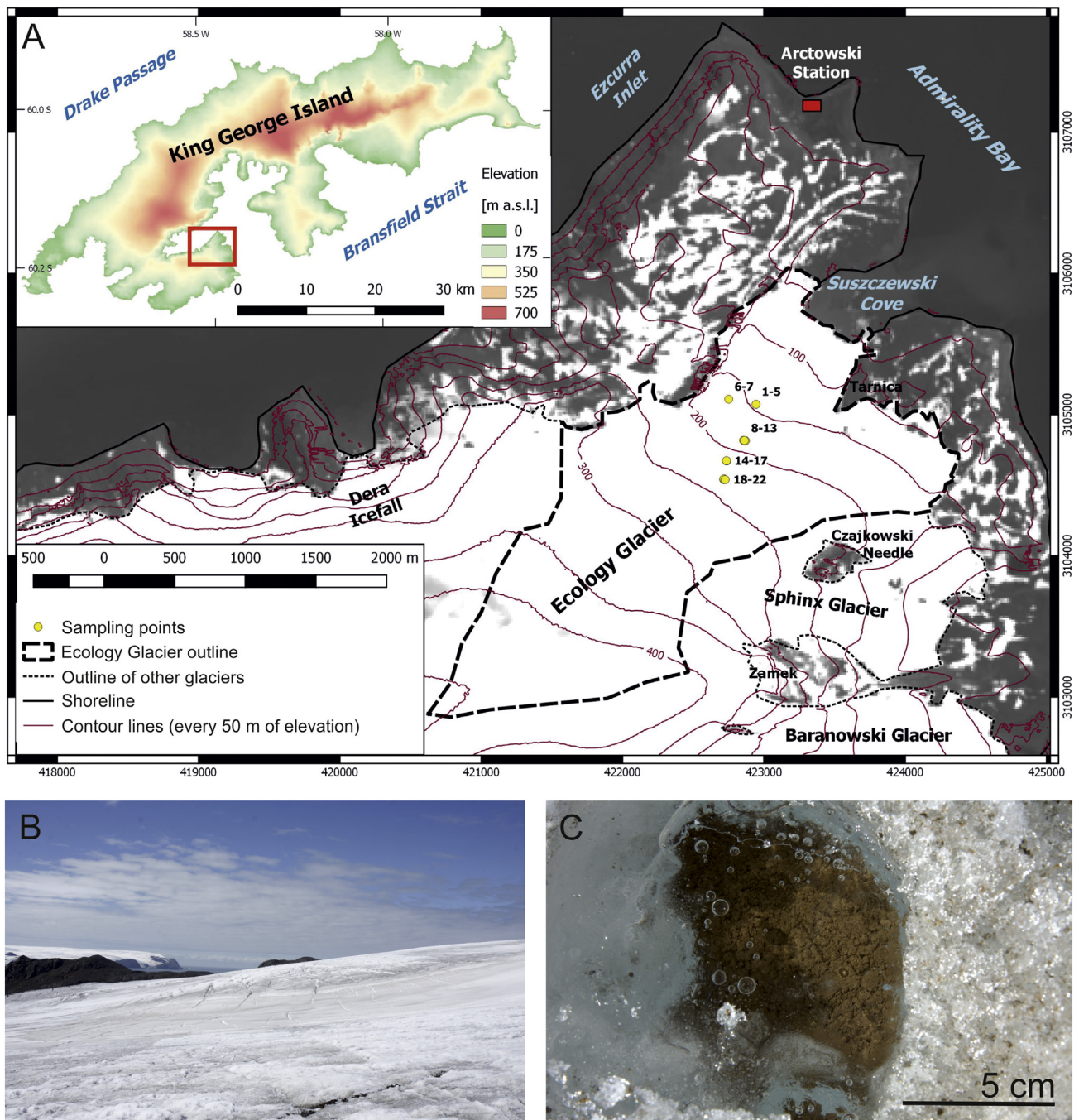


Fig. 1. A: Map of study area. Reference system: WGS 1984, UTM zone 21S; background: LANDSAT Image, acquisition date: 2014/01/16, courtesy of USGS; contour lines based on Braun et al. (2016). B: surface of Ecology Glacier in midsummer 2017, C: cryoconite hole on Ecology Glacier.

noted in the frontal retreat rate that has decelerated after 2002, however the main driver of glacier front displacements is subglacial/submarine topography at the glacier cliff (Pełlicki et al., 2017). Overall frontal changes of Ecology Glacier are moderate with the average rate ca. $0.019 \text{ km}^2 \text{ y}^{-1}$ measured in the periods 1961–1996 and 2007–2012 (Kejna et al., 1998; Sobota et al., 2015). Most ice masses of King George Island located below 400 m a.s.l. are at the pressure melting point (Blindow et al., 2010). Shallow temperature profiles confirm the existence of temperate ice on Ecology Glacier (Sobota et al., 2015).

2.2. Sampling

In total, 23 melted cryoconite holes were sampled on Ecology Glacier during fieldwork of January 2017. Cryoconite holes were located at

three altitudes all within the ablation zone (Fig. 1) including: 1. 128–142 m a.s.l. with 7 holes, 2. 168–172 m a.s.l. with 6 holes, and 3. 201–221 m a.s.l. with 9 holes. Altitudes and measurements of the depth and height of the water column were made for 22 cryoconite holes (hole no. 23 was sampled beyond of the transect). Additional parameters, such as depth, diameter, length and width of cryoconite holes, were measured when possible (diameter for spherical holes, width and length for irregularly shaped holes) with a ruler. Cryoconite material (0.5 to 1.3 cm^3) was collected using sterile plastic Pasteur pipettes and transferred to 15 cm^3 tubes and immediately preserved with 96% ethylene alcohol. Samples were stored frozen and transported to laboratories in Poland. All 23 samples were used for faunistic analyses and organic matter measurements. For phylogenetic and radiometric analyses, 12 and 10 samples were used, respectively. In the laboratory,

after the cryoconite material had settled in the tubes (i.e., after at least 30 min), only the sediment was collected for the analysis. The amount of sediment used for analysis was estimated based on the measure of the plastic tube.

2.3. Organic matter

The amount of organic matter in cryoconite was measured as a percentage weight loss through combustion at 550 °C for 3 h following drying at 50 °C for 24 h.

2.4. Microscopic observations and estimation of cyanobacteria and algae biomass

Cyanobacteria and algae were identified, counted, and measured with a Nikon Eclipse TE2000-S digital microscope. Taxa were archived through NIS (Imaging Software NIS – Elements BR on VGA). The biomass of cyanobacteria and algae for each hole was calculated as the total cell volume per unit area (standard coverslip). Mean cell volume was estimated by measuring the size of 50–100 cells for each species. To ensure accuracy of measurements, each sample was counted three to six times and thus cell concentrations (cells/cm³) are mean values of the repeated counts. The biomass of cyanobacteria and algae for each sample was calculated as the total cell volume per unit area (standard coverslip). Every time under standard coverslip 100 µl of the cryoconite was mounted and analysed (after Yoshimura et al., 1997, modified). The taxonomy of cyanobacteria and algae was based on Hoek et al. (1995) and identification of cyanobacterial and algal species followed Krammer and Lange-Bertalot (1991a, 1991b), Hindak (1996), Komárek and Anagnostidis (2005), Coesel and Meesters (2007), Van de Vijver et al. (2010) and John and Rindi (2015). Fig. S2 contains diatom shells without chloroplast for better visibility of diagnostic features.

2.5. Microfauna extraction and identification

The material was homogenised by shaking the vials and transferred into Petri dishes (ø 8.5 cm) and entire cryoconite material was scanned for microfauna using a stereomicroscope (Olympus BZ51). On the bottom of each Petri dish, parallel thin lines at 5-mm intervals were drawn with a black marker for precise scanning (5 mm corresponds to a visible image at 30× magnification). The entire cryoconite material was scanned for microfauna using a stereomicroscope (Olympus BZ51). Subsequently, all individuals were isolated and counted. The density of animals was calculated per 1 cm³ of cryoconite.

Representatives of the nanorchestid mite populations were cleared in KOH or Nesbitt's fluid, mounted on microslides in Hoyer's medium, examined using an Olympus BX50 phase-contrast microscope and subsequently identified following the keys of Strandmann (1982) and Booth (1984).

To delimit rotifer species, total genomic DNA was extracted from 14 separate individuals (selected from six cryoconite holes) using the method described in Dabert et al. (2008) and Mironov et al. (2012). DNA was isolated with the DNeasy Blood and Tissue Kit (Qiagen GmbH, Hilden, Germany) following the protocol of Dabert et al. (2008). A fragment of the mitochondrial cytochrome c oxidase subunit I (COI) gene was amplified with a LCO1490 forward primer (5'-GGTCAACAAATCATAAAGATATTTGG-3') and HCO2198 reverse primer (5'-TAAACTCAGGGTGACCAAAAAATCA-3') (Folmer et al., 1994). Amplification of DNA fragments (PCR) for a total volume of 10 µl was carried out with the following protocol: 5 µl Type-it Microsatellite PCR Kit (Qiagen), 0.25 µM of each primer, 4 µl of the DNA template and 0.5 µl water. For PCR, a thermocycling profile with one cycle of 5 min at 95 °C followed by 5 steps of 30 s each at 95 °C, 60 s at 45 °C, 1 min at 72 °C, and 30 steps 30 s at 95 °C, 60 s at 50 °C and 60 s at 72 °C with a final step of 5 min at 72 °C for all amplicons. Samples containing single, uniform 700-bp bands were purified with exonuclease I and fast alkaline

phosphatase (Fermentas). The amplicons were sequenced with the BigDye Terminator v3.1 kit and ABI Prism 3130xl Genetic Analyzer (Applied Biosystems) following the manufacturer's instructions. The identity of COI sequences was verified with BLAST (Altschul et al., 1990) against the NCBI database. Sequences were processed in BioEdit ver. 7.2.5 (Hall, 1997). Delimitation and identification of the rotifer species as independently evolving entities (IEEs) was conducted employing the GMYC model (Pons et al., 2006; Fujisawa and Barraclough, 2013) on both ultrametric trees constructed in BEAST 1.10.4 and Bayesian trees constructed in MrBayes 3.2, and then converted to ultrametric ones using the *chronopl* (lambda = 100) function in RStudio software (R Core Team, 2018). GMYC analysis was performed in RStudio using the 'paran' and 'splits' packages (Supplementary Material, Appendix A, Figs. 5 and 6). The following sequences were utilised in the analysis: KJ543594-KJ543597 and KP869999 belongs to *Macrotrachela jankoi* (Iakovenko et al., 2015), and KP870000 belongs to *Macrotrachela* aff. *jankoi*, and as an out group, *Floscularia melicerta* GenBank ID EU499896 (FLM) was used (Iakovenko et al., 2015). The remaining sequences are new and described in the results.

Slides with animals are deposited in the Department of Animal Taxonomy and Ecology, Adam Mickiewicz University in Poznań, Poland.

2.6. Identification and measurements of radionuclides

Owing to location and separation by cold oceanic waters of Antarctic Peninsula, it is a suitable region for analysing transport of contaminants in the environment. The Antarctic ecosystem is of great interest in estimating global environmental pollution caused by nuclear detonation tests and accidents. In order to identify radionuclides, time of their deposition and links between biotic and abiotic characteristics of supraglacial ecosystems, we identified radionuclides in glacier of Maritime Antarctic for the first time. ¹³⁷Cs and ²¹⁰Pb activity was determined with a broad energy germanium detector (BEGe), BE5030. The activities of ¹³⁷Cs were determined using its emission peak at 662 keV, and the emission peak at 46.6 keV was employed to determine the activities of ²¹⁰Pb. The activities of the ²³⁸Pu, ²³⁹⁺²⁴⁰Pu, ²⁴¹Am, ^{234,238}U and ^{230,232}Th radionuclides were determined in 0.48 to 0.85 g of the dried samples. The samples were dissolved with mineral acids and resultant liquid samples underwent radiochemical separation and concentrations of all alpha isotopes. The procedure is extensively described elsewhere by Łokas et al. (2010, 2013, 2018). The full sequential radiochemical procedure and gamma analyses were verified employing soil reference material (IAEA 385). The results were in strong agreement with the recommended values. After further radiochemical purification procedure, the ²⁴⁰Pu/²³⁹Pu atomic ratio was measured through a Neptune MC-ICP-MS in accordance to Łokas et al. (2018). The reference date for ²¹⁰Pb and ¹³⁷Cs activities is 1 January 2017.

2.7. Data processing

We tested relations between continuous variables using Spearman-rank correlation (assumption for the Pearson correlation were violated). To test differences of the mean for elevations groups we used a Kruskal-Wallis rank-sum test. In case of significant results of Kruskal-Wallis, we used post hoc Dunn's test with Bonferroni-corrected alpha level. To determine central tendency we used mean and the standard error (SE) for normally distributed data, while for the variables with the distribution that deviated from normal we used the median. To assess variance for normally distributed data, we used Standard Deviation (SD), while the variables with the distribution that deviated from normal we used the Interquartile Range (IQR). Moreover, we tested evenness of a community of algae using Pielou Diversity index J based on the Shannon-Wiener index. The analysis was processed using R software (R Core Team, 2018) and MVSP 3.1 software (Kovach 1985–1999).

3. Results

Mean diameter and total depth for sampled cryoconite holes on Ecology Glacier in January 2017 were 10.0 ± 2.5 , 95%CI (14.98, 16.21) and 15.9 ± 4 , 95%CI (10.48, 11.22) cm. All measurements of cryoconite holes are presented in the Table S1. The collected cryoconite consisted mostly of fine mineral grains and infrequent minute cryoconite granules (Fig. S3). Cryoconite holes located in lower altitude were deeper than those located in the middle and the highest altitude (Dunn's test, $p = 0.014$ and $p = 0.002$, respectively).

Organic matter varied between 5.4% and 7.6% ($median = 6.72$, $IQR = 0.79$, $n = 23$), but without any clear gradient with the elevation (Fig. S1). There was no significant correlation between organic matter content and depth of cryoconite holes ($\rho = 0.21$, $df = 20$, $p = 0.14$). Likewise, there was no correlation between organic matter and total photoautotrophic biomass ($\rho = -0.077$, $p = 0.8119$). However, a significant difference in means of organic matter were found between first and second group (lowest and middle altitude) of samples, with higher organic matter content in middle (Kruskal-Wallis $\chi^2 = 8.026$, $df = 2$, $p = 0.02$; Dunn's test $p = 0.0089$).

Each cryoconite hole was characterised by relatively low biodiversity (4 to 10 species). Overall, 4 species of Chlorophyta, 4 species of Cyanobacteria, 7 species of Bacillariophyceae and 2 unidentified cysts (Fig. 2, S2; Tables S2, S3) were found with relatively even distribution (Diversity index (J')) 0.347 to 1.013. In most cryoconite holes, the predominant cyanobacterial species included *Pseudanabaena frigida*, *Leptolyngbya* sp. 1, *Leptolyngbya* sp. 2 and *Komvophoron* sp., diatoms *Microcostatus* sp., and filamentous green algae *Klebsormidium flaccidum*. *Microcostatus* sp. and *Pseudanabaena frigida* dominated all holes (Fig. S2). The biomass of Bacillariophyceae was significantly higher than that of Cyanobacteria (Dunn's test, $p < 0.001$) and Chlorophyta (Dunn's test, $p = 0.004$). However, there were no differences between Chlorophyta and Cyanobacteria biomass (Dunn's test, $p = 0.052$) (Fig. 2, Tables S2, S3). There were no differences in total biomass of

photoautotrophs among 3 elevational patches (Kruskal-Wallis $\chi^2 = 1.2603$, $df = 2$, $p = 0.5325$).

Among invertebrates, only 3 species of Rotifera (according to the GenBank search using BLAST algorithm and our sequence data: representatives of Philodinavidae family, relative of *Adineta* sp. and *Macrotrachela* aff. *jankoi* (Iakovenko et al., 2015)) and 1 species of Acari (*Nanorchestes nivalis* (Trouessart, 1914) sensu Judson (1995)) were observed, but while rotifers were present in every hole ($median = 37$, $IQR = 60.5$, $n = 23$), mites were found in 30% of the holes ($median = 0$, $IQR = 1$, $n = 23$) (Figs. 3–5; Table S1). Sequences for rotifers obtained in this study are deposited in GenBank under accession numbers: MT181011–MT181018; MT180985–MT180987; MT180992–MT180993. Two rotifer species did not match any rotifer sequences in GenBank and may potentially be new to science (Figs. 5, S5, S6). We found a marginally significant differences in densities of rotifers among elevational groups (Kruskal-Wallis $\chi^2 = 6.0825$, $df = 2$, $p = 0.05$, Fig. 4).

Artificial and natural radionuclides observed in the samples included ^{137}Cs , $^{239+240}\text{Pu}$, ^{241}Am , ^{210}Pb , $^{234,238}\text{U}$ and $^{230,232}\text{Th}$ (Table 1, Fig. S4). Significantly higher concentrations of ^{210}Pb (Dunn's test, $p = 0.0131$) were associated with samples located at the middle elevation than the lowest one. Isotopic ratios of $^{238}\text{Pu}/^{239+240}\text{Pu}$, $^{239+240}\text{Pu}/^{137}\text{Cs}$ $^{241}\text{Am}/^{239+240}\text{Pu}$ indicate that analysed cryoconite material could be of about 60–70 years old.

4. Discussion

Our study presents baseline data on biotic and abiotic characteristics of cryoconite holes for a glacier in Maritime Antarctica. Herein, we present data on morphology, organic matter content, primary producers, top consumers and contamination of radionuclides (proxy for long-range transport of anthropogenic originated contaminations) for cryoconite holes on Ecology Glacier sampled in 2017. Ecology Glacier is located close to the Polish Antarctic Station, "Arctowski", on King George Island (thus supporting easy logistics) and for years was in the

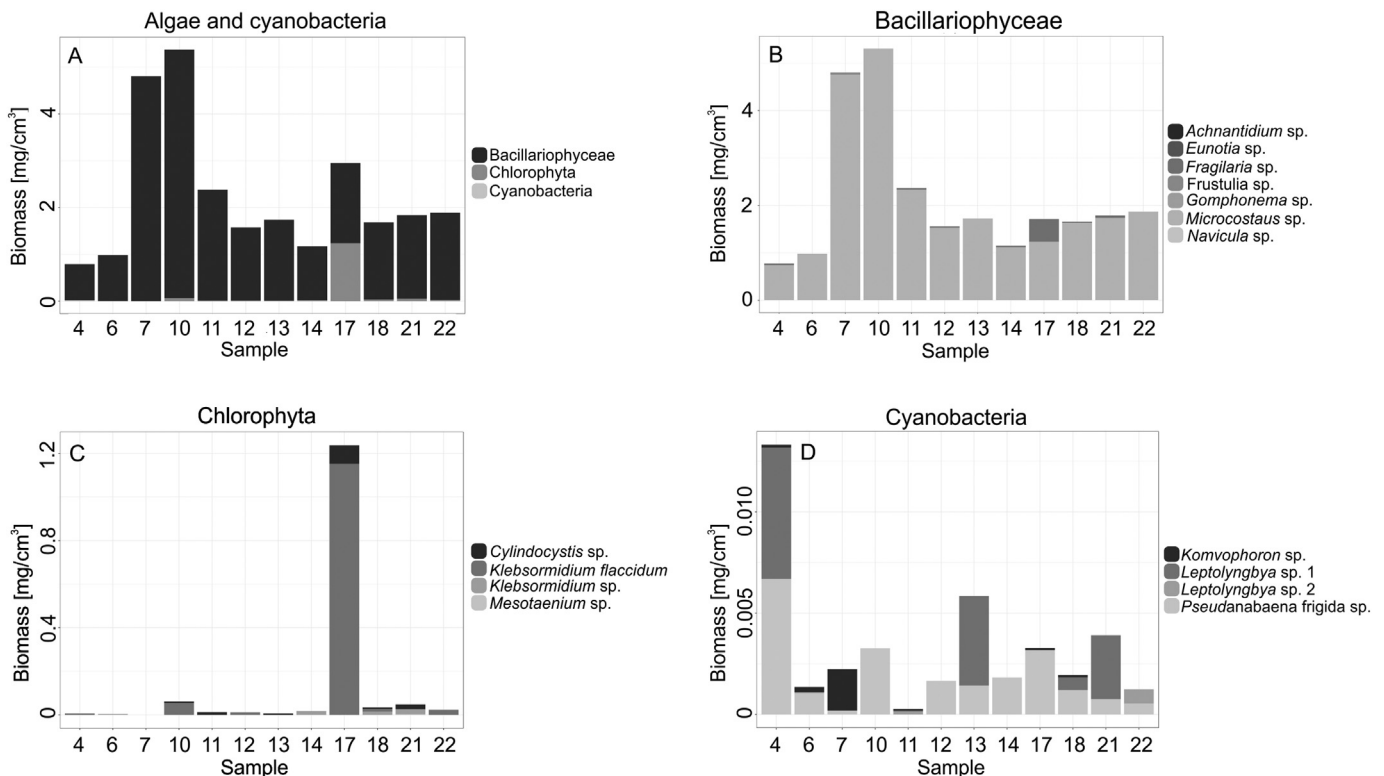


Fig. 2. Biomass of cyanobacteria and algae in cryoconite holes from Ecology Glacier in mid Austral Summer 2017. A: Comparison of biomass between Bacillariophyceae, Chlorophyta and Cyanobacteria, B: Biomass of particular taxa among Bacillariophyceae, C: Biomass of particular taxa among Chlorophyta, D: Biomass of particular taxa among Cyanobacteria.

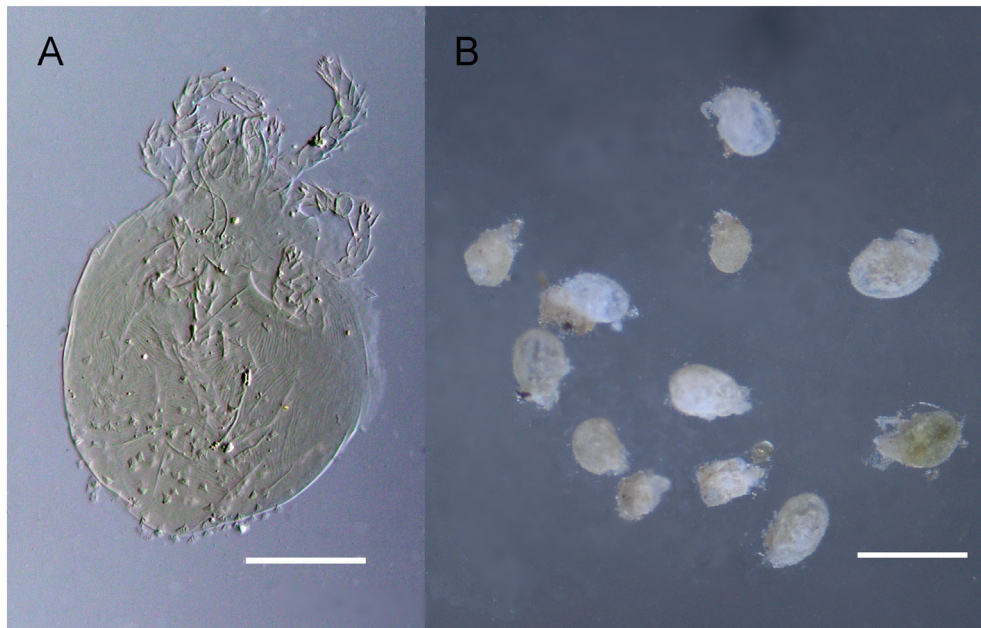


Fig. 3. *Nanorchestes nivalis* (Trouessart, 1914) from cryoconite holes: A- tritonymph mounted on slide (scalebar 100 µm), B- nymphs and few adults (scalebar 500 µm).

focus of biologists (e.g., [Dziewit et al., 2013](#); [Mieczan et al., 2013](#); [Grzesiak et al., 2015](#)), ecologists ([Zawierucha et al., 2019](#)), glaciologists (e.g., [Bintanja, 1995](#); [Sobota et al., 2015](#); [Pętllicki et al., 2017](#)) and geomorphologists ([Sziło and Bialik, 2017](#)) (Table S5). Taking into account the entirety of the literature on the biota of Ecology Glacier published until now, as well as the present study, 4 cyanobacterial taxa, 11 algae, 20 ciliates and 4 metazoans (Rotifera, Acari) have been reported (Table S4; see also subsequent results and discussion).

4.1. Cryoconite holes

The results of this study showed that cryoconite holes located at lower elevations on the Ecology Glacier have larger depth. The same phenomenon was observed in the Thule Area, (Greenland) by [Gajda \(1958\)](#), who showed various depths of cryoconite holes at different distances from the terminus of valley glacier. Following [Gajda \(1958\)](#), this

effect could be caused by more energy available for melting at lower elevations of a glacier. Nevertheless, our study on Ecology Glacier and the study by [Gajda \(1958\)](#) cover a distance of <1 km. An opposite pattern but at a larger scale (4 km on valley glacier – Sermikavsak, Greenland) was shown by [Gribbon \(1979\)](#), who found deeper cryoconite holes in the upper part of glaciers. The results of this study and that of [Gajda's \(1958\)](#) may stem from local variations of their surface structure: samples were taken from visually different types of ice, as opposed to [Gribbon \(1979\)](#), who made measurements in each location on visually similar ice patches. Summarising the aforementioned results, cryoconite holes located further from the edge of a glacier are characterised by moving their equilibrium-depths deeper into the ice. A detailed explanation of these phenomena has been proposed by [Gribbon \(1979\)](#), however we did not observe this pattern, which in case of our sampling, might be related to smaller elevational gradient. Detailed formation of cryoconite holes, their forms, and depths were earlier discussed by

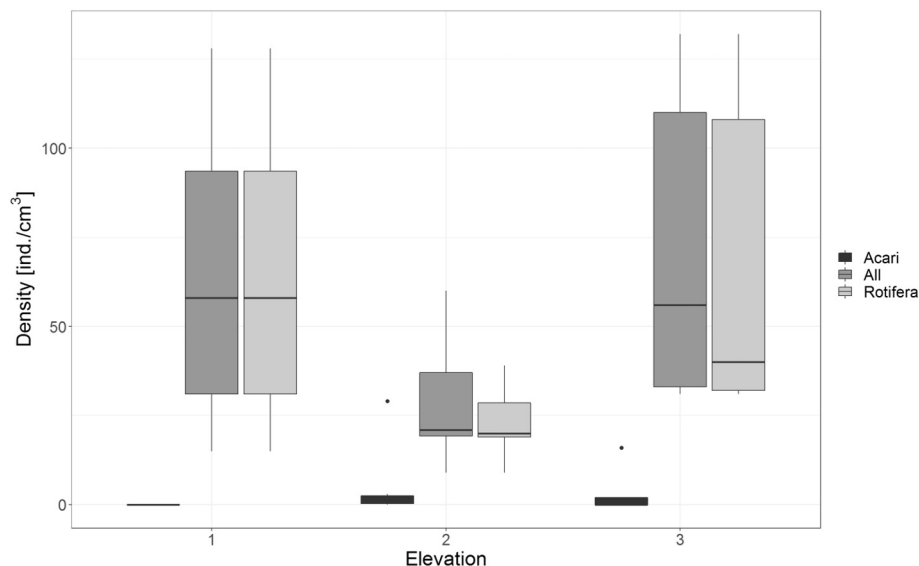


Fig. 4. Densities of Acari, Rotifera and both in cryoconite holes from Ecology Glacier in mid Austral Summer 2017. Boxes denote 25th, 50th, and 75th percentiles; whiskers represent the lowest and highest datum within the 1.5 interquartile ranges of the lower and upper quartiles. Densities of mites on Ecology Glacier in 2018 are described in [Zawierucha et al. \(2019\)](#).

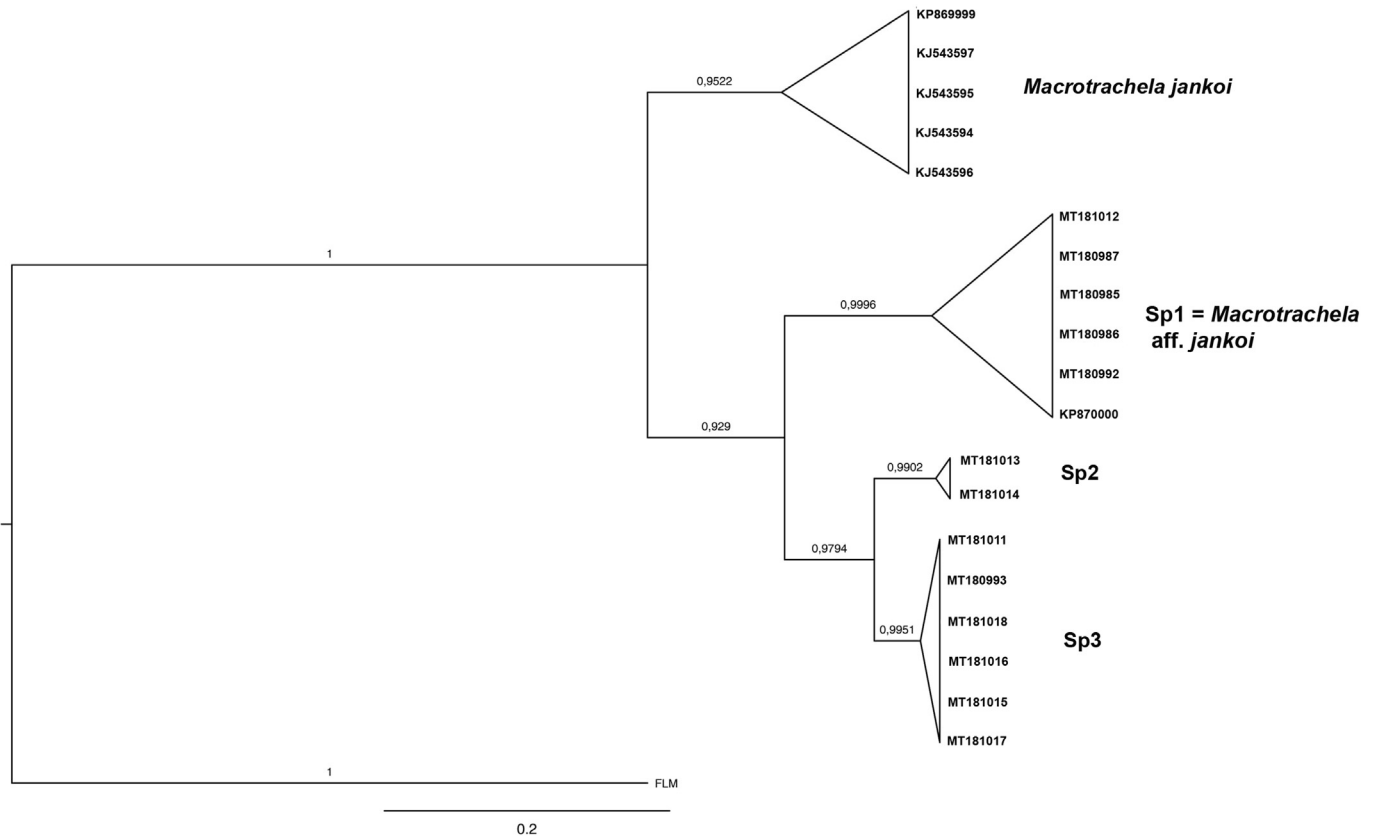


Fig. 5. Species delimitation of rotifers found in cryoconite from Ecology Glacier (sp. 1, sp. 2, sp. 3), and their phylogenetic relationships to some Antarctic rotifer species (*Macrotrachela jankoi* s. str., *M. aff. jankoi*). Each clade represents a unique species (Independent Evolutionary Entity, IEE).

Sharp (1949). Cryoconite holes on Ecology Glacier are smaller in diameter and size, and with thin layer of ice lid (or lacking such) during sampling, compared to those in the Antarctic McMurdo Dry Valleys (Fountain et al., 2004). However, they are similar in size and depth as well as being open (or with very thin layer of ice) to those in Arctic Svalbard archipelago (Zawierucha et al., 2016b). This indicates that physical processes like flushing, ablation, solar radiation influencing size and shape of cryoconite holes in maritime Antarctic are similar to those found in Arctic insular climate.

4.2. Organic matter

The organic matter content in cryoconite holes from around the world can vary from <2% (e.g., Tyndal Glacier, Patagonia) to >18% (e.g., Thule Ice Ramp, Greenland) (Gerdel and Drouet, 1960; Takeuchi et al., 2001a). However, an average organic matter (7%) content in cryoconite from holes (Cook et al., 2015) is similar to that found in our

study (6.7%). Although relatively low in our cryoconite samples, the content of organic matter has been shown to play a key role in many geochemical and biological processes in the cryosphere. Not only does it provide substrates for heterotrophic organisms, but also lowers ice albedo and binds various pollutants (Cook et al., 2015; Łokas et al., 2016, 2018). Contrary to other observations (Porazinska et al., 2004; Stibal et al., 2010; Langford et al., 2014), we did not observe elevational pattern of organic matter content. These findings might reflect relative flatness of the sampled elevational gradient on Ecology Glacier, small sampling area, and possibly the timing of sampling. Significantly higher organic matter content in holes at the middle elevation is hard to explain. It is possible that opposing forces drive the productivity of organic matter (like an autochthonous and allochthonous input), and wash-out (removal) operate across elevations. Lower elevations may have more organic matter, but stronger wash-out obscures this, while wash-out is lower at higher elevations, along with lower productivity. This could result in intermediate effect. Organic matter content on Ecology Glacier is higher than on glaciers in Continental Antarctic (Foreman et al., 2007), which might be related to higher productivity of glaciers located close to marine ecosystems.

4.3. Algae and cyanobacteria

We observed that cryoconite holes on Ecology Glacier are mostly algae-dominated systems. These findings were rather unexpected as cyanobacteria are considered cryoconite hole ecosystem engineers (Takeuchi et al., 2001a, 2001b; Hodson et al., 2008; Cook et al., 2015). They produce extracellular polymeric substances that stick together mineral and organic matter on glaciers to form granules commonly observed in the Arctic and High Alpine (Takeuchi et al., 2001a; Hodson et al., 2010; Langford et al., 2014; Cook et al., 2015). We observed only small and rare cryoconite granules under a stereomicroscope, suggesting

Table 1
List of radionuclides detected in cryoconite holes on Ecology Glacier in 2017. SEM - Standard error of mean.

Radionuclide	Source	Minimum	Maximum	Mean (N = 10)	SEM
¹³⁷ Cs	Anthropogenic	185 ± 14	350 ± 22	266	18.257
²³⁸ Pu	Anthropogenic	0.30 ± 0.04	1.08 ± 0.11	0.62	0.077
²³⁹⁺²⁴⁰ Pu	Anthropogenic	2.97 ± 0.24	7.32 ± 0.53	5.41	0.484
²⁴¹ Am	Anthropogenic	1.69 ± 0.13	5.02 ± 0.28	3.57	0.364
²¹⁰ Pb	Natural	1400 ± 100	2600 ± 200	1873	138.126
²³⁴ U	Natural	12 ± 1	18 ± 1	14.45	0.618
²³⁸ U	Natural	9 ± 1	17 ± 1	13	0.746
²³⁰ Th	Natural	15 ± 1	22 ± 2	19	0.731
²³² Th	Natural	8 ± 1	11 ± 1	9	0.266

that binding properties of cyanobacteria to form granules are marginal on Ecology Glacier (Fig. S3). This likely reflects communities and biomass dominated by algae over cyanobacteria. The dominance of algae over cyanobacteria in holes is generally not common, or perhaps not well known, since studies of cryoconite communities generally focus on their diversity rather than biomass (Pittino et al., 2018). We cannot exclude that inland ice sheets and small valley glaciers with significantly big inputs of dust or englacial outcropping minerals may favor cyanobacteria that bind particles and form granules; tide water glaciers located in big fjords may receive more aqueous nutrients that favor algae. However such assumptions need further studies.

The number of taxa of cyanobacteria and algae on Ecology Glacier appears consistent with previous studies in Continental Antarctica (Wharton Jr et al., 1981; Porazinska et al., 2004; Sommers et al., 2017). Slightly higher numbers of cyanobacterial taxa were found in previous studies on cryoconite holes in Continental Antarctic. Wharton Jr et al., 1981 and Porazinska et al. (2004) reported seven and six taxa of cyanobacteria, respectively. However, it should be taken into account that the authors investigated several glaciers (Wharton Jr et al., 1981; Porazinska et al., 2004), thus differences may be attributed to broader study sites. In the case of algae, Porazinska et al. (2004) did not describe them in glaciers located in the McMurdo Dry Valleys. However, Sommers et al. (2017) recently showed five taxa of algae via environmental sequencing. Among all taxa of cyanobacteria and algae revealed in our study, only one was previously found in cryoconite holes on Continental Antarctica (*Pseudanabaena frigida* (Fritsch)) by Sommers et al. (2017, 2019). We did not find any of the diatom taxa reported by Stanish et al. (2012) from glaciers in Antarctic Taylor Valley, who found the two dominant cryoconite hole genera, *Diademsis* and *Muelleria*. In turn, the observed taxa of cyanobacteria and algae on Ecology Glacier corresponds better to that found on Chilean and Arctic glaciers than to Continental Antarctic cryoconite holes (Takeuchi et al., 2001a; Porazinska et al., 2004; Stibal et al., 2006; Sommers et al., 2017, 2019; Zawierucha et al., 2018).

Certain taxa of algae may be specially adapted to life within the cryoconite holes, other are opportunistic (Cameron et al., 2012; Mueller et al., 2001; Yallop and Anesio, 2010). In the Arctic, where the holes are frequently hydrologically connected and lacking an ice lid, the community function and composition appears to be influenced by surface hydrology (Zawierucha et al., 2018). Ecology Glacier in Maritime Antarctica might be such equivalent example.

Stanish et al. (2013) have shown that cryoconite holes in McMurdo Dry Valleys located on glaciers within the most productive hydrological basin and closest to the Ross Sea, had the highest diatom richness. Authors claimed that glaciers at the coastal end of the Antarctic Taylor valley receive more aeolian inputs from the local area and probably collect more biological material, including diatoms, from stream beds and exposed lake shores (Stanish et al., 2013). It supports our observations on biotic community on Ecology Glacier, which due to proximity of sea sprays bearing nutrients and delivery of mineral matter from surrounding mountains may favor diatoms.

The dominance of algae over cyanobacteria in cryoconite holes from Ecology Glacier which are mostly shallow and with thin and fragile ice lid (or without lid) potentially negatively affect cyanobacterial survivorships in quickly changing and unstable environment. Compared to Bacillariophyceae, Cyanobacteria are slow growing and more sensitive to disturbance like sediment load, flushing and mixing of water (Tang et al., 1997). Although not all Cyanobacteria may fix nitrogen directly from the atmosphere, open holes could also experience nitrogen deposition (e.g., via snow and rain precipitation) stimulating algal growth, but inhibiting cyanobacterial activities (Telling et al., 2012), especially in dynamic cryoconite holes on a small glacier. None of those mechanisms, however, have been well studied indicating the scope of work that lays ahead.

4.4. Animals

The rotifers and mites found in our samples are filter- and liquid- or suspension-feeders, feeding on bacteria, algae and perhaps detritus. For the first time on Ecology Glacier, a species of a mite (*Nanorchestes nivalis*) is fully confirmed (as a new metazoan group in cryoconite) and identified. The species have been previously reported from the Maritime Antarctic (Petermann I., Anvers I., Deception I. (South Shetland), Monroe I. (South Orkney)) and the Subantarctic (Candlemas I. (South Sandwich), South Georgia I. - Trouessart, 1914, Strandtmann, 1982).

Antarctic nanorchestid mites have been observed in soil and mosses (e.g., Marshall and Pugh, 1996; Convey and Smith, 1997; Hogg and Stevens, 2002; Niemi et al., 2002), but never fully confirmed as persistent residents in cryoconite holes (Zawierucha et al., 2015, 2019). According to Rounsevell and Greenslade (1988), *Nanorchestes* spp. are characterised by granulations in the cuticle, an adaptation to life in very humid or water habitats, where the roughness of the surface by trapping layers of air allows for respiration and protects against freezing. The ability to survive freezing up to -41°C was demonstrated by Fitzsimons (1971). *Nanorchestes antarcticus* Strandtmann, 1963 was observed to maintain normal motoric activity between -23°C and $+31^{\circ}\text{C}$ (Fitzsimons, 1971). More importantly, *Nanorchestes* spp. can feed on algae (Schuster and Schuster, 1977) indicating preadaptations for living in icy ecosystems such as cryoconite holes, especially those on Ecology Glacier dominated by diatoms. Therefore, the presence of *N. nivalis* on Ecology Glacier, does not appear merely accidental, especially that more recently (2018) sediments retrieved from the same glacier contained the same mite (Zawierucha, Buda, Magowski - personal observation, Zawierucha et al., 2019). Taking into account that representatives of *N. nivalis* are relatively small in comparison to other Antarctic mites and under stereomicroscope resemble organic granules, it is easy to overlook these animals (Fig. 3 A, B). Most probably, the lack of aforementioned physiological adaptations in a vast majority of mites prevents them from colonising glaciers, and single individual findings elsewhere are rather fortuitous in cryoconite holes. A good example is a single individual of the oribatid tritonymph, *Platynothrus punctatus* (C.L. Koch, 1879) (Acari: Oribatida), which was detected only on one (Hansbreen) among six glaciers on Svalbard, indicating an accidental windblown faunal element (Olszanowski - personal observation). We confirmed the presence of various instars of mites in cryoconite holes on Ecology Glacier during two seasons. Definitely, our results show that *N. nivalis* on Ecology Glacier can be a persistent resident in cryoconite holes.

Invertebrates like tardigrades and rotifers are common in cryoconite holes in polar regions acting as top consumers (Zawierucha et al., 2015, 2018, 2019). Rotifer diversity found on Ecology Glacier is lower than in other reports on cryoconite holes in the Arctic, and higher than in the Continental Antarctic. Porazinska et al. (2004) observed 2 rotifer species on glaciers in the McMurdo Dry Valleys, while De Smet and Van Rompu (1994) found 7 species of rotifers on a glacier on Svalbard. Densities of rotifers on Ecology Glacier are greater than in the McMurdo Dry Valleys (Porazinska et al., 2004) and comparable with those in the Arctic (Zawierucha et al., 2018).

Acutuncus antarcticus (Richters, 1904) is a common Antarctic tardigrade found previously in cryoconite holes (Cesari et al., 2016; Porazinska et al., 2004), however, not a single specimen of any tardigrade species was found in our study, nor in samples collected in 2018 (personal observation, Zawierucha et al., 2019). On Ecology Glacier, a single specimen of *A. antarcticus* was detected in a cryoconite hole material collected by J. Grzesiak in 2009. Absence of tardigrades remains unclear, while they are common in Arctic and Continental Antarctic cryoconite holes (Porazinska et al., 2004; Zawierucha et al., 2016a,b, 2018, 2019).

4.5. Radionuclides

The main sources of plutonium in the Southern Hemisphere were French and British nuclear tests in the Southern Pacific (Mururoa),

Australia (Woomera) and Indian Ocean (Monte Bello) areas. Another and most significant source of ^{238}Pu (90%) in the Antarctic is accidental burn-up of the SNAP-9A satellite in the atmosphere over Madagascar in 1964. In addition, the $^{238}\text{Pu}/^{239+240}\text{Pu}$ ratios in few samples suggest contributions from local or perhaps more recent trace of Pu of a different origin.

Occurrence of ^{241}Am is related to directly by nuclear explosions, and its environmental activity is increasing, because of the decay product of the fallout beta emitter ^{241}Pu ($T_{1/2} = 14.4$ yr). Therefore the $^{241}\text{Am}/^{239+240}\text{Pu}$ ratio can rise to the range of 0.32–0.42. The ratio can be also as high in the Southern Hemisphere as 0.80 (2017) based on the high-yield US nuclear tests in 1953 at Bikini Atoll, Marshal Island and Enewetak Atoll (Jia et al., 1999). It was calculated from the $^{241}\text{Pu}/^{239+240}\text{Pu}$ activity ratio in 1953. To what extent these pollutants affect cryoconite communities is still unknown, but warrants further research.

There is ongoing interest in radioactivity of Antarctic terrestrial and marine ecosystems (Roos et al., 1994; Jia et al., 1999, 2000; Desideri et al., 2003; Giuliani et al., 2003; Mietelski et al., 2000, 2008; Szufa et al., 2018), including ice shelves (Koide et al., 1979). Radionuclide activity concentrations in cryoconite holes may reach much higher values than in surrounding glacier habitats including mosses and lichens. Recently cryoconite was suggested as efficient accumulator of radionuclides in the high mountain regions due to being significantly more radioactive than the matrices usually adopted for the environmental monitoring of radioactivity (Łokas et al., 2018; Baccolo et al., 2020). Indeed, our results of radioactivity of cryoconite from Ecology Glacier indicate the same phenomenon for Antarctic region. Prolonged exposure of cryoconite to atmospheric dust and the presence of cryophilic organisms and organic matter may lead to a build-up of radionuclide levels (Fig. 6). Comparing our data with the maximum activity concentrations of ^{137}Cs in mosses (50 Bq kg^{-1}), lichens (162 Bq kg^{-1}) (Jia et al., 1999) and soils (30 Bq kg^{-1}) (Schuller et al., 1993), values from cryoconite holes are 2 to 3 times higher. A similar trend was observed in activity concentrations of ^{238}Pu , $^{239+240}\text{Pu}$ and ^{241}Am in mosses (0.21 Bq kg^{-1} , 0.91 Bq kg^{-1} , 0.61 Bq kg^{-1}), lichens (0.75 Bq kg^{-1} , 4.6 Bq kg^{-1} , 1.9 Bq kg^{-1}) and soils (0.003 Bq kg^{-1} , 0.019 Bq kg^{-1} , 0.010 Bq kg^{-1}) (Jia et al., 1999).

Studies around the world indicate that radionuclides are actively trapped in cryoconite and ice. First studies on artificial radionuclides content on glaciers were conducted by Jaworowski et al. (1978) who showed that artificial radioactive isotopes are stored in ice. Cryoconite is a kind of biogenic sediment formed when combination of the

processes acting in the supraglacial zone leads to mixing and interaction of mineral particulate matter of local and remote origin with organic compounds, bacteria and algae (Takeuchi et al., 2010, 2001 a, b). We suspect that anthropogenic (artificial) radionuclides stored in ice, during melting are released and accumulate in microbes and fungi and up the food chain in microinvertebrates. When viruses lyse cells, they release radionuclides into the cryoconite again. We found that the highest contents of lead was observed in the middle altitude with highest organic matter that may effectively accumulate and recycle artificial radionuclides (Łokas et al., 2016). However, clarifying of this assumption need further studies. Values of activity ratios (Łokas et al., 2018; Baccolo et al., 2017) in cryoconite collected from holes suggest their yearly biogeochemical recycling, also on Ecology Glacier for >70 years when first artificial radionuclides appeared (Fig. 6). Presence of artificial radionuclides on Ecology Glacier indicates that mineral material in cryoconite cannot be old englacial origin and most probably is derived within last 70 years (windblown from mountains and forefields). High level of radionuclides could be related to algae and cyanobacteria, but effects of such bioaccumulation on glaciers needs closer attention.

5. Summary

- We observed variation of cryoconite holes depth, organic matter content, Rotifera counts as well as lead-210 concentration. Such heterogeneity may result from the specific morphology of the glacier surface, distance from terminus (potential transport of aerosols) as well as altitude.
- Depth of cryoconite holes on Ecology Glacier in January 2017 was related to elevation and increased towards the glacier margin.
- Distribution of organic matter content was homogenous and unrelated to hole morphology.
- Seventeen taxa of algae and cyanobacteria, three taxa of rotifers, and one of Acari were found.
- Cryoconite holes on Ecology Glacier were dominated by Bacillariophyceae. This predominance most probably prevents formation of glacier cryoconite granules.
- A suspension-feeding mite species was observed and identified for the first time in cryoconite holes.
- Densities of animals were more similar to Arctic than to Continental Antarctic cryoconite holes.
- Radionuclides have been likely stored on Ecology Glacier since 1950s and these radionuclides are most probably recycled in cryoconite each season by microbial communities.

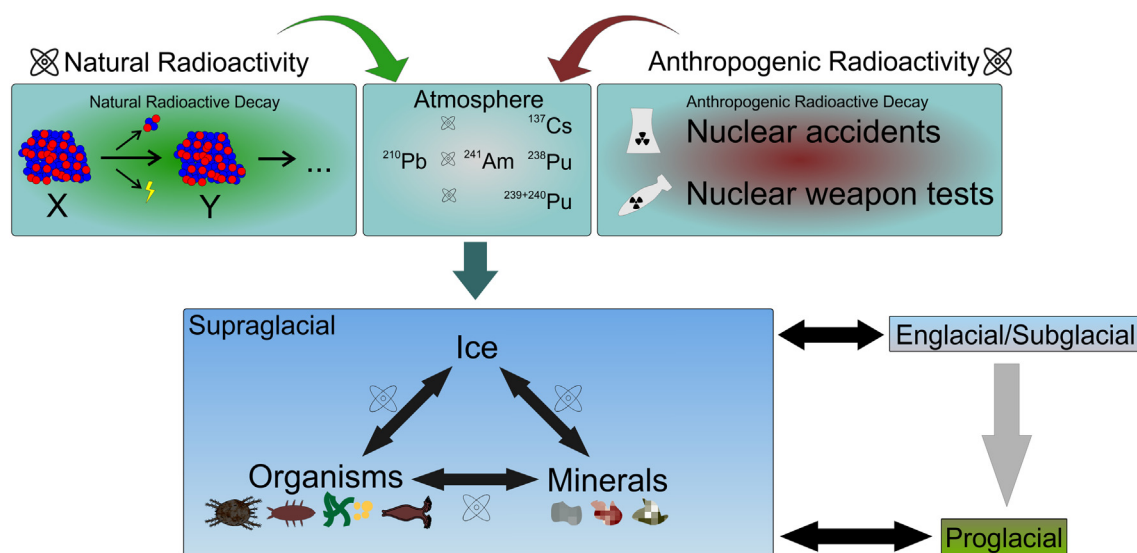


Fig. 6. Scheme presents sources of radionuclides and their connections with ice, organisms and minerals.

- Taking into account all the literature and recently presented data, Ecology Glacier may constitute robust glacier model for comparisons of glacial biodiversity between South America and Continental Antarctic.
- All biotic characteristics of cryoconite holes on Ecology Glacier presented in this study are specific functions of time and space (locality) of sampling in Maritime Antarctic.

CRediT authorship contribution statement

Jakub Buda: Data curation, Formal analysis, Methodology, Writing - original draft, Writing - review & editing. **Edyta Łokas:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Mirosława Pietryka:** Data curation, Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Dorota Richter:** Data curation, Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Wojciech Magowski:** Data curation, Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Nataliia S. Iakovenko:** Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Dorota L. Porazinska:** Investigation, Writing - original draft, Writing - review & editing. **Tomasz Budzik:** Funding acquisition, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Mariusz Grabiec:** Conceptualization, Funding acquisition, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Jakub Grzesiak:** Investigation, Writing - original draft, Writing - review & editing. **Piotr Klimasyk:** Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Paweł Gaca:** Formal analysis, Investigation, Methodology, Writing - original draft, Writing - review & editing. **Krzysztof Zawierucha:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Writing - original draft, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2020.138112>.

References

- Altschul, S.F., Gish, W., Miller, W., Myers, E.W., Lipman, D.J., 1990. Basic local alignment search tool. *J. Mol. Biol.* 215, 403–410. [https://doi.org/10.1016/S0022-2836\(05\)80360](https://doi.org/10.1016/S0022-2836(05)80360).
- Anesio, A.M., Laybourn-Parry, J., 2012. Glaciers and ice sheets as a biome. *Trends Ecol. Evol.* 27, 219–225.
- Anesio, A.M., Hodson, A.J., Fritz, A., Psenner, R., Sattler, B., 2009. High microbial activity on glaciers: importance to the global carbon cycle. *Glob. Chang. Biol.* 15, 955–960.
- Artaxo, P., Rabello, M.L., Maenhaut, W., Grieken, R.V., 1992. Trace elements and individual particle analysis of atmospheric aerosols from the Antarctic peninsula. *Tellus B* 44, 318–334.
- Baccolo, G., Di Mauro, B., Massabò, D., Clemenza, M., Nastasi, M., Delmonte, B., Prata, M., Prati, P., Previtali, E., Maggi, V., 2017. Cryoconite as a temporary sink for anthropogenic species stored in glaciers. *Sci. Rep.* 7, 9623.
- Baccolo, G., Łokas, E., Gaca, P., Massabò, D., Ambrosini, R., Azzoni, R.S., Clason, C., Di Mauro, B., Franzetti, A., Nastasi, M., Prata, M., Prati, P., Previtali, E., Delmonte, B., Maggi, V., 2020. Cryoconite: an efficient accumulator of radioactive fallout in glacial environments. *Cryosphere* 14, 657–672.
- Bagshaw, E.A., Tranter, M., Fountain, A.G., Welch, K.A., Basagic, H.J., Lyons, W.B., 2007. Biogeochemical evolution of cryoconite holes on Canada glacier, Taylor Valley, Antarctica. *J. Geophys. Res.* 112, G04S35.
- Bagshaw, E.A., Tranter, M., Wadham, J.L., Fountain, A.G., Mowlem, M., 2011. High-resolution monitoring reveals dissolved oxygen dynamics in an Antarctic cryoconite hole. *Hydrol. Process.* 25, 2868–2877.
- Bagshaw, E.A., Tranter, M., Fountain, A.G., Welch, K.A., Basagic, H.J., Lyons, W.B., 2013. Are cryoconite holes a significant source of C, N and P to the downstream depauperate ecosystems of the McMurdo dry valleys? *Arct. Antarct. Alp. Res.* 45, 1–15.
- Bintanja, R., 1995. The local surface energy balance of the ecology glacier, King George Island, Antarctica: measurements and modelling. *Antarct. Sci.* 7, 315–325.
- Birkenmajer, K., Francalanci, L., Peccerillo, A., 1991. Petrological and geochemical constraints on the genesis of Mesozoic–Cenozoic magmatism of King George Island, South Shetland Islands, Antarctica. *Antarct. Sci.* 3, 293–308.
- Blindow, N., Suckro, S., Ruckamp, M., Braun, M., Breuer, B., Saurer, H., Simoes, J., Schindler, M., Lange, M., 2010. Geometry and thermal regime of the King George Island ice cap, Antarctica, from GPR and GPS. *Ann. Glaciol.* 51, 103–109.
- Booth, R.G., 1984. A new species of mite in the genus *Nanorchestes* (Acari, Prostigmata) from Signy Island, South Orkney Islands. *British Antarctic Survey Bulletin* 63, 111–116.
- Braun, M., Gossmann, H., 2002. Glacial changes in the areas of Admiralty Bay and Potter Cove, King George Island, maritime Antarctica. In: Beyer, L., Bolter, M. (Eds.), *Geocology of Antarctic Ice-free Coastal Landscapes*. 2002. Springer-Verlag, Berlin Heidelberg Ecological studies 154.
- Braun, M., Saurer, H., Vogt, S., Simões, J.C., Gossmann, H., 2001. The influence of large-scale atmospheric circulation on surface energy balance on the ice cap of King George Island. *Int. J. Climatol.* 21, 21–36.
- Braun, H., Betsch, T., Seehaus, T., 2016. King George Island TanDEM-X DEM, link to GeoTIFF. Institut für Geographie, Friedrich-Alexander-Universität. Erlangen-Nürnberg, PANGAEA <https://doi.org/10.1594/PANGAEA.863567>.
- Cameron, K.A., Hodson, A.J., Osborn, A.M., 2012. Structure and diversity of bacterial, eukaryotic and archaeal communities in glacial cryoconite holes from the Arctic and the Antarctic. *FEMS Microbiol. Ecol.* 82, 254–267.
- Cesari, M., McInnes, S., Bertolani, R., Rebecchi, L., Guidetti, R., 2016. Genetic diversity and biogeography of the south polar water bear *Acutuncus antarcticus* (Eutardigrada: Hypsibiidae) – evidence that it is a truly pan-Antarctic species. *Invertebr. Syst.* 30, 635–649.
- Coesel, P.F.M., Meesters, J., 2007. Desmids of the Lowlands. *Mesotaeniaceae and Desmidiaceae of the European Lowlands*. KNNV Publishing (351 pp).
- Convey, P., 2013. Maritime Antarctic climate change: signals from terrestrial biology. *Antarctic Research Series*, 145–158 <https://doi.org/10.1029/ar079p0145>.
- Convey, P., Smith, R.L.L., 1997. The terrestrial arthropod fauna and its habitats in northern Marguerite Bay and Alexander Island, maritime Antarctica. *Antarct. Sci.* 9, 12–26.
- Cook, J., Edwards, A., Takeuchi, N., Irvine-Fynn, T., 2015. Cryoconite. The dark biological secret of the cryosphere. *Prog. Phys. Geogr.* 40, 66–111.
- Dabert, J., Ehrnsberger, R., Dabert, M., 2008. *Glaucalgae tytonis* sp. nov. (Analgidae: Xolalgidae) from the barn owl *Tyto alba* (Strigiformes: Tytonidae): compiling morphology with DNA barcode data for taxa descriptions in mites (Acari). *Zootaxa* 1719, 41–52.
- Dasty, H., Kraus, H.J., Thaler, K., 2003. Redescription and Notes on the Biology of the Glacier Tardigrade *Hypsibius klebelsbergi* Mihelcic, 1959 (Tardigrada). Based on Material from Ötztal Alps, Austria. 100. Mitteilungen Hamburgisches Zoologisches Museum und Institut, pp. 77–100.
- De Smet, W.H., Van Rompu, E.A., 1994. Rotifera and Tardigrada from some cryoconite holes on a Spitsbergen (Svalbard) glacier. *Belgian Journal of Zoology* 124, 27.
- Desideri, D., Giuliani, S., Testa, C., Triulzi, C., 2003. 90Sr, 137Cs, 238Pu, 239+240Pu and 241Am levels in terrestrial and marine ecosystems around the Italian base in Antarctica. *J. Radioanal. Nucl. Chem.* 258, 221–225.
- Dziewit, L., Grzesiak, J., Ciok, A., Nieckarz, M., Zdanowski, M.K., Bartosik, D., 2013. Sequence determination and analysis of three plasmids of *Pseudomonas* sp. GLE121, a

- psychrophile isolated from surface ice of ecology glacier (Antarctica). *Plasmid* 70, 254–262.
- Edwards, A., Rassner, S.M., Anesio, A.M., Worgan, H.J., Irvine-Fynn, T.D., Wyn Williams, H., Sattler, B., Wyn Griffith, G., 2013. Contrasts between the cryoconite and ice-marginal bacterial communities of Svalbard glaciers. *Polar Res.* 32, 19468.
- Ferron, F.A., Simões, J.C., Aquino, F.E., Setzer, A.W., 2004. Air temperature time series for King George Island, Antarctica. *Pesquisa Antártica Brasileira* 4, 155–169.
- Fitzsimons, J.M., 1971. Temperature and three species of Antarctic arthropods. *Pacific Insects Monographs* 25, 127–135.
- Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol. Mar. Biol. Biotechnol.* 3, 294–299.
- Foreman, C.M., Sattler, B., Mikuchi, J.A., Porazinska, D.L., Priscu, J.C., 2007. Metabolic activity and diversity of cryoconites in the Taylor Valley, Antarctica. *Aquat. Geochem.* 10, 239–268.
- Fountain, A., Tranter, M., Nylen, T.H., Lewis, K.J., Mueller, D.R., 2004. Evolution of cryoconite holes and their contribution to melt water runoff from glaciers in the McMurdo dry valleys, Antarctica. *J. Glaciol.* 50, 35–45.
- Franzetti, A., Navarra, F., Tagliaferri, I., Gandolfi, I., Bestetti, G., Minora, U., Azzoni, R.S., Diolaiuti, G., Smiraglia, C., Ambrosini, R., 2017. Potential sources of bacteria colonizing the cryoconite of an Alpine glacier. *PLoS One* 12, e0174786.
- Fujisawa, T., Barraclough, T.G., 2013. Limiting species using single-locus data and the generalized mixed yule coalescent approach: a revised method and evaluation on simulated data sets. *Syst. Biol.* 62, 707–724.
- Gajda, R.T., 1958. Cryoconite phenomena on the Greenland ice cap in the Thule area. *Can. Geogr.* 3, 35–44.
- Gerdel, R.W., Drouet, F., 1960. The cryoconite of the Thule area, Greenland. *Trans. Am. Microsc. Soc.* 79, 256–272.
- Giuliani, S., Triulzi, C., Vaghi, M., 2003. Anthropogenic radionuclides in plants, animals and their environments in Antarctica. *Морской биологический журнал* 2 (551.35:539.163).
- Gribbon, P.W.F., 1979. Cryoconite holes on Sermikavak, west Greenland. *J. Glaciol.* 22, 177–181.
- Grzesiak, J., Zdanowski, M.K., Górniak, D., Świątecki, A., Alksandrak-Piekarczyk, T., Szatraj, K., Sasin-Kurowska, J., Nieckarz, M., 2015. Microbial community changes along the ecology glacier ablation zone (King George Island, Antarctica). *Polar Biol.* 38, 2069–2083. <https://doi.org/10.1007/s00300-015-1767-z>.
- Hall, T.A., 1997. BIOEDIT: a user-friendly biological sequence alignment editor and analysis program for windows 95/98/NT. *Nucleic Acids Symp. Ser.* 41, 95–98.
- Hindak, F., 1996. Key to the unbranched filamentous green algae (Ulotrichineae, Ulotrichales, Chlorophyceae). *Bulletin Slovenskej botanickej spoločnosti pri SAV, Bratislava*, p. 77.
- Hodson, A., Anesio, A.M., Tranter, M., Fountain, A., Osborn, M., Priscu, J., Laybourn-Parry, J., Sattler, B., 2008. Glacial ecosystems. *Ecol. Monogr.* 78, 41–67.
- Hodson, A., Bøggild, C., Hanna, E., Huybrechts, P., Langford, H., Cameron, K., Houldsworth, A., 2010. The cryoconite ecosystem on the Greenland ice sheet. *Ann. Glaciol.* 51, 123–129.
- Hodson, A., Nowak, A., Sabacka, M., Jungblut, A., Navarro, F., Pearce, D., Ávila-Jiménez, M.L., Convey, P., Vieira, G., 2017. Climatically sensitive transfer of iron to maritime Antarctic ecosystems by surface runoff. *Nat. Commun.* 8, 14499.
- Hoek, C., Mann, D.G., Johns, H.M., 1995. *Alga: An Introduction to Phycology*. 623. Great Britain at University Press, Cambridge.
- Hogg, I.D., Stevens, M.I., 2002. Soil fauna of Antarctic coastal landscapes. *Geocology of Antarctic Ice-Free Coastal Landscapes*. Springer, Berlin, Heidelberg, pp. 265–280.
- Iakovenko, N.S., Smykja, J., Convey, P., Kašparová, E., Kozeretka, I.A., Trokhymets, V., Dykyy, I., Plewka, M., Devetter, M., Duriš, Z., Janko, K., 2015. Antarctic bdelloid rotifers: diversity, endemism and evolution. *Hydrobiologia* 761, 5–43.
- Jaworowski, Z., Kownacka, L., Grotowski, K., Kwiatkowski, K., 1978. LEAD-210 from nuclear explosions in the environment. *Nucl. Technol.* 37, 159–166.
- Jia, G., Triulzi, C., Marzano, F.N., Belli, M., Sansone, U., Vaghi, M., 1999. Plutonium, ²⁴¹Am, ⁹⁰Sr, and ¹³⁷Cs concentrations in some antarctic matrices. *Biol. Trace Elem. Res.* 71, 349–357.
- Jia, G., Triulzi, C., Marzano, F.N., Belli, M., Vaghi, M., 2000. The fate of plutonium, ²⁴¹Am, ⁹⁰Sr and ¹³⁷Cs in the Antarctic ecosystem. *Antarct. Sci.* 12, 141–148.
- John, D.M., Rindi, F., 2015. Freshwater algae of North America. *Ecology and classification*. *Aquatic Ecology*, pp. 375–427.
- Judson, M., 1995. Identity of the Antarctic mite *Gainia nivalis* Trouessart (Acari, Nanorchestidae). *Bulletin du Muséum national d'histoire naturelle*. 17, pp. 83–86.
- Kejna, M., Laska, K., Caputa, Z., 1998. Recession of ecology glacier (King George Island) in the period 1961–1996. *Polish Polar Studies* 121–128.
- Kejna, A., Sobota, I., Araźny, A., 2012. Warunki meteorologiczne w rejonie Stacji Arctowskiego (Wyspa Króla Jerzego, Antarktyka) w okresie 19.01–19.02.2012 roku. *Problemy Klimatologii Polarnej* 103–116.
- Knap, W.H., Oerlemans, J., Cabée, M., 1996. Climate sensitivity of the ice cap of King George Island, South Shetland Islands, Antarctica. *Ann. Glaciol.* 23, 154–159.
- Koide, M., Michel, R., Goldberg, E.D., Herron, M.M. & Langway Jr, C.C. (1979). Depositional history of artificial radionuclides in the Ross ice shelf, Antarctica. *Earth Planet. Sci. Lett.* 44, 205–223.
- Komárek, J. & Anagnostidis, K. (2005). Cyanoprokaryota; Oscillatoriales II. In: Büdel, A.B., Krammer, K.L. & Lange-Bertalot, H. (1986). Bacillariophyceae 2/1. Naviculaceae. In: H. Ettl, J. Krienitz, G. Gärtner, & Schagerl, M. (eds). Süßwasserflora von Mitteleuropa, vol. 19.2, Spektrum Akademischer Verlag, pp. 759.
- Kovach, W.L., 1985–1999. *MVSP PLUS*. Pentraeth, UK, version 3.1.
- Krammer, K., Lange-Bertalot, H., 1991a. Bacillariophyceae 2/3. Centrales, Fragilariaceae, Eunotiaceae. In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora von Mitteleuropa. Gustav Fischer Stuttgart, New York, p. 576.
- Krammer, K., Lange-Bertalot, H., 1991b. Bacillariophyceae 2/4. Achnanthesaceae, Kritische, Ergänzungen zu Navicula (Lineolatae) und Gomphonema Gesamtliteraturverzeichnis. In: Ettl, H., Gerloff, J., Heynig, H., Mollenhauer, D. (Eds.), Süßwasserflora von Mitteleuropa. Gustav Fischer Stuttgart, New York, p. 437.
- Langford, H.J., Irvine-Fynn, T.D.I., Edwards, A., Banwart, S.A., Hodson, A.J., 2014. A spatial investigation of the environmental controls over cryoconite aggregation on Longyearbreen glacier, Svalbard. *Biogeosciences* 11, 5365–5380.
- Łokas, E., Mietelski, J.W., Kleszcz, K., Tomankiewicz, E., 2010. A sequential procedure for determining ²³⁸Pu, ²³⁹⁺²⁴⁰Pu, ²⁴¹Am, ⁹⁰Sr, U and Th activities in soils and peats from Spitsbergen. *Nukleonika* 55, 195–199.
- Łokas, E., Mietelski, J.W., Ketterer, M.E., Kleszcz, K., Wachniew, P., Michalska, S., Miecznik, M., 2013. Sources and vertical distribution of ¹³⁷Cs, ²³⁸Pu, ²³⁹⁺²⁴⁰Pu and ²⁴¹Am in peat profiles from Southwest Spitsbergen. *Appl. Geochem.* 28, 100–108.
- Łokas, E., Zaborska, A., Kolicka, M., Różycki, M., Zawierucha, K., 2016. Accumulation of atmospheric radionuclides and heavy metals in cryoconite holes on an Arctic glacier. *Chemosphere* 160, 162–172. <https://doi.org/10.1016/j.chemosphere.2016.06.051>.
- Łokas, E., Zawierucha, K., Cwanek, A., Szufa, K., Gaca, P., Mietelski, J.W., Tomankiewicz, E., 2018. The sources of high airborne radioactivity in cryoconite holes from the Caucasus (Georgia). *Sci. Rep.* 8, 10802. <https://doi.org/10.1038/s41598-018-29076-4>.
- Łokas, E., Zaborska, A., Sobota, I., Gaca, P., Milton, A., Kocurek, P., Cwanek, A., 2019. Airborne radionuclides and heavy metals in high Arctic terrestrial environment as the indicators of sources and transfers of contamination. *Cryosphere Discuss.* <https://doi.org/10.5194/tc-2019-34>.
- Marshall, D.J., Pugh, P.J., 1996. Origin of the inland Acari of continental Antarctica, with particular reference to Dronning Maud Land. *Zool. J. Linnean Soc.* 118, 101–118.
- Marsz, A.A., Styszyńska, A. (Eds.), 2000. The Main Features of the Climate Region the Polish Antarctic Station H. Arctowski (West Antarctica, South Shetland Islands, King George Island). Wyższa Szkoła Morska, Gdynia, pp. 1–264 (in Polish).
- Martianov, V., Rakusa-Suszczewski, S., 1989. Ten years of climate observations at the Arctowski and Bellingshausen stations (King George Is., South Shetlands, Antarctica). *Global Change. regional research centres*, pp. 80–87.
- Miecznik, T., Górniak, D., Świątecki, A., Zdanowski, M., Tarkowska, M., Adamczuk, M., 2013. Vertical microzonation of ciliates in cryoconite holes in ecology glacier, King George Island. *Polish Polar Research* 34, 201–212.
- Mietelski, J., Gaca, P., Olech, M., 2000. Radioactive contamination of lichens and mosses collected in south Shetlands and Antarctic peninsula. *J. Radioanal. Nucl. Chem.* 245, 527–537.
- Mietelski, J.W., Olech, M.A., Sobiech-Matura, K., Howard, B.J., Gaca, P., Zwolak, M., Błażej, S., Tomankiewicz, E., 2008. ¹³⁷Cs, ⁴⁰K, ²³⁸Pu, ²³⁹⁺²⁴⁰Pu and ⁹⁰Sr in biological samples from King George Island (southern Shetlands) in Antarctica. *Polar Biol.* 31, 1081–1089.
- Mironov, S.V., Dabert, J., Dabert, M., 2012. A new feather mite species of the genus *Proctophylloides* Robin, 1877 (Astigmata: Proctophylloidae) from the long-tailed tit *Aegithalos caudatus* (Passeriformes: Aegithalidae) – morphological description with DNA barcode data. *Zootaxa* 3253, 54–61.
- Mueller, D.R., Vincent, W.F., Pollard, W.H., Fritsen, C.H., 2001. Glacial Cryoconite Ecosystems: A Bipolar Comparison of Algal Communities and Habitats Nova Hedwigia. 123 pp. 173–197.
- Navarro, F., Jonsell, U., Corcuera, M., Martin-Espanol, A., 2013. Decelerated mass loss of Hurd and Johnsons glaciers, Livingston Island, Antarctic peninsula. *J. Glaciol.* 59, 115–128.
- Niemi, R., Uusitalo, M., Lintinen, P., 2002. *Nanorchestes* Tøpssent and Trouessart, 1890 and *Eupodes* Koch, 1836 (Acari: Prostigmata) from Vestfjella mountain range, Antarctica. *Entomologica Fennica* 13, 236–240.
- Oliva, M., Navarro, F., Hrbáček, F., Hernández, A., Nývlt, D., Pereira, P., Ruiz-Fernández, J., Trigo, R., 2017. Recent regional climate cooling on the Antarctic peninsula and associated impacts on the cryosphere. *Sci. Total Environ.* 580, 210–223.
- Petlicki, M., Szilo, J., MacDonell, S., Vivero, S., Bialik, R., 2017. Recent deceleration of the ice elevation change of ecology glacier (King George Island, Antarctica). *Remote Sens.* 9, 520. <https://doi.org/10.3390/rs9060520>.
- Pittino, F., Maglio, M., Gandolfi, I., Azzoni, R.S., Diolaiuti, G., Ambrosini, R., Franzetti, A., 2018. Bacterial communities of cryoconite holes of a temperate alpine glacier show both seasonal trends and year-to-year variability. *Ann. Glaciol.* 1–9.
- Pons, J., Barraclough, T.G., Gomez-Zurita, J., Cardoso, A., Duran, D.P., Hazell, S., Kamoun, S., Sumlin, W.D., Vogler, A.P., 2006. Sequence-based species delimitation for the DNA taxonomy of undescribed insects. *Syst. Biol.* 55, 595–609.
- Porazinska, D.L., Fountain, A.C., Nylen, T.H., Tranter, M., Virginia, R.A., Wall, D.H., 2004. The biodiversity and biogeochemistry of cryoconite holes from McMurdo Dry Valley glaciers, Antarctica. *Arct. Antarct. Alp. Res.* 36, 84–91.
- Quayle, W.C., Peck, L.S., Peat, H., Ellis-Evans, J.C., Harrigan, P.R., 2002. Extreme responses to climate change in Antarctic Lakes. *Science* 295, 645. <https://doi.org/10.1126/science.1064074>.
- R Core Team, 2018. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna <https://www.R-project.org>.
- Rakusa-Suszczewski, S., Mietus, M., Piasecki, J., 1993. Weather and climate. In: Rakusa-Suszczewski, S. (Ed.), *The Maritime Antarctic Coastal Ecosystem of Admiralty Bay*. Warsaw, Polish Academy of Sciences, pp. 19–25.
- Robinson, S.A., Wasley, J., Tobin, A.K., 2003. Living on the edge—plants and global change in continental and maritime Antarctica. *Glob. Chang. Biol.* 9, 1681–1717.
- Roos, P., Holm, E., Persson, R.B.R., Aarkrog, A., Nielsen, S.P., 1994. Deposition of ²¹⁰Pb, ¹³⁷Cs, ²³⁹⁺²⁴⁰Pu, ²³⁸Pu, and ²⁴¹Am in the Antarctic peninsula area. *J. Environ. Radioact.* 24, 235–251.
- Rounsevell, D.E., Greenslade, P., 1988. Cuticle structure and habitat in the *Nanorchestidae* (Acari: Prostigmata). *Hydrobiologia* 165, 209–212.
- Samui, G., Antony, R., Thamban, M., 2018. Chemical characteristics of hydrologically distinct cryoconite holes in coastal Antarctica. *Ann. Glaciol.* <https://doi.org/10.1017/aog.2018.30>.
- Schuller, P., Løvgreen, C., Handl, J., 1993. ¹³⁷Cs concentration in soil, prairie plants, and milk from sites in southern Chile. *Health Phys.* 64, 157–161.

- Schuster, R., Schuster, U., 1977. Ernährungs- und fortpflanzungs-biologische Studien an der Milbenfamilie Nanorchestidae. Zool. Anz. 199, 89–94.
- Segawa, T., Yonezawa, T., Edwards, A., Akiyoshi, A., Tanaka, S., Uetake, J., Irvine-Fynn, T., Fukui, K., Li, Z., Takeuchi, N., 2017. Biogeography of cryoconite forming cyanobacteria on polar and Asian glaciers. J. Biogeogr. 44, 2849–2861.
- Sharp, R.P., 1949. Studies of superglacial debris on valley glaciers. Am. J. Sci. 247, 289–315.
- Sobota, I., Kejna, M., Arażny, A., 2015. Short-term mass changes and retreat of the ecology and Sphinx glacier system, King George Island, Antarctic peninsula. Antarct. Sci. 27, 500–510.
- Sommers, P., Darcy, J.L., Gendron, E.M.S., Stanish, L.F., Bagshaw, E.A., Porazinska, D.L., Schmidt, S.K., 2017. Diversity patterns of microbial eukaryotes mirror those of bacteria in Antarctic cryoconite holes. FEMS Microbiol. Ecol. 94. <https://doi.org/10.1093/femsec/fix167>.
- Sommers, P., Darcy, J.L., Porazinska, D.L., Gendron, E.M.S., Fountain, A.G., Zamora, F., Vincent, K., Cawley, K.M., Solon, A.J., Vimercati, L., Ryder, J., Schmidt, S.K., 2019. Comparison of microbial communities in the sediments and water columns of frozen cryoconite holes in the McMurdo dry valleys. Antarctica. Front. Microbiol. 10. <https://doi.org/10.3389/fmicb.2019.00065>.
- Stanish, L.F., Bagshaw, E.A., McKnight, D.M., Fountain, A.G., Tranter, M., 2013. Environmental factors influencing diatom communities in Antarctic cryoconite holes. Environ. Res. Lett. 8, 045006. <https://doi.org/10.1088/1748-9326/8/4/045006>.
- Stibal, M., Šabacká, M., Kaštovská, K., 2006. Microbial communities on glacier surfaces in Svalbard: impact of physical and chemical properties on abundance and structure of cyanobacteria and algae. Microb. Ecol. 52, 644.
- Stibal, M., Lawson, E.C., Lis, G.P., Mak, K.M., Wadham, J.L., Anesio, A.M., 2010. Organic matter content and quality in supraglacial debris across the ablation zone of the Greenland ice sheet. Ann. Glaciol. 51, 1–8.
- Stibal, M., Schostag, M., Cameron, K.A., Hansen, L.H., Chandler, D.M., Wadham, J.L., Jacobsen, C.S., 2015. Different bulk and active bacterial communities in cryoconite from the margin and interior of the Greenland ice sheet. Environ. Microbiol. Rep. 7, 293–300.
- Stibal, M., Bradley, J.A., Edwards, A., Hotaling, S., Zawierucha, K., Rosvold, J., Lutz, S., Cameron, K.A., Mikucki, J.A., Kohler, T.J., Šabacká, M., Anesio, A.M., 2020. Glacial ecosystems are essential to understanding biodiversity responses to glacier retreat. Nat. Ecol. & Evol. <https://doi.org/10.1038/s41559-020-1163-0>.
- Strandtmann, R.W., 1982. Notes on *Nanorchestes* V. two new species of *Nanorchestes* (Acari: Nanorchestidae) from the Antarctic peninsula and South Atlantic islands. Pacific Insects 24, 252–258.
- Szilo, J., Bialik, R.J., 2017. Bedload transport in two creeks at the ice-free area of the Baranowski glacier, King George Island, West Antarctica. Polish Polar Research 38, 21–29.
- Szufa, K.M., Mielinski, J.W., Anczkiewicz, R., Sala, D., Olech, M.A., 2018. Variations of plutonium isotopic ratios in Antarctic ecosystems. J. Radioanal. Nucl. Chem. 318, 1511–1518.
- Takeuchi, N., Kohshima, S., Shiraiwa, T., Kubota, K., 2001a. Characteristics of cryoconite (surface dust on glaciers) and surface albedo of a Patagonian glacier, Tyndall glacier, southern Patagonia icefield. Bull. Glaciol. Res. 18, 65–69.
- Takeuchi, N., Kohshima, S., Goto-Azuma, K., Koerner, R.M., 2001b. Biological characteristics of dark colored material (cryoconite) on Canadian Arctic glaciers (Devon and penny ice caps). Proceedings of the Memoirs of the National Institute of Polar Research, Special Issue. 54, pp. 495–505.
- Takeuchi, N., Nishiyama, H., Li, Z., 2010. Structure and formation process of cryoconite granules on Ürtmqi glacier no. 1, Tien Shan, China. Ann. Glaciol. 51, 9–14.
- Tang, E.P., Tremblay, R., Vincent, W.F., 1997. Cyanobacterial dominance of polar freshwater ecosystems: are high-latitude mat-formers adapted to low temperature. J. Phycol. 33, 171–181.
- Tedstone, A.J., Bamber, J.L., Cook, J.M., Williamson, C.J., Fettweis, X., Hodson, A.J., Tranter, M., 2017. Dark ice dynamics of the south-west Greenland ice sheet. Cryosphere 11, 2491–2506.
- Telling, J., Anesio, A.M., Tranter, M., Stibal, M., Hawkings, J., Irvine-Fynn, T., Hodson, A., Butler, C., Wadham, J., 2012. Controls on the autochthonous production and respiration of organic matter in cryoconite holes on high Arctic glaciers. Journal of Geophysical Research: Biogeosciences 117 (G1).
- Trouessart, E., 1914. Acariens. Deuxième Expédition Antarctique Française (1908–1910), commandée par le Dr. Jean Charcot. Sciences naturelles. Documents scientifique. Masson, Paris, pp. 1–16.
- Turner, J., Lu, H., White, I., King, J., Phillips, T., Hosking, J., Bracegirdle, T., Marshall, G., Mulvaney, R., Deb, P., 2016. Absence of 21st century warming on Antarctic peninsula consistent with natural variability. Nature 535, 411–415.
- Van de Vijver, B., Ector, L., de Haan, M., Zidarova, R., 2010. The genus *Microcostatus* in the Antarctic region. Diatom Research 25, 417–429.
- Wharton Jr., R.A., Vinyard, W.C., Parker, B.C., Simmons Jr., G.M., Seaburg, K.G., 1981. Algae in cryoconite holes on Canada glacier in southern Victoria land, Antarctica. Phycologia 20, 208–211.
- Williamson, C.J., Anesio, A.M., Cook, J., Tedstone, A., Poniecka, E., Holland, A., Fagan, D., Tranter, M., Yallop, M.L., 2018. Ice algal bloom development on the surface of the Greenland ice sheet. FEMS Microbiol. Ecol. 94, fty025.
- Yallop, M.L., Anesio, A.M., 2010. Benthic diatom flora in supra-glacial habitats: a generic level comparison. Annales de Glaciologie 51, 15–22.
- Yoshimura, Y., Kohshima, S., Ohtani, S., 1997. A community on snow algae on a Himalayan glacier: change of algal biomass and community structure with altitude. Arct. Alp. Res. 29, 126–137.
- Zawierucha, K., Kolicka, M., Takeuchi, N., Kaczmarek, Ł., 2015. What animals can live in cryoconite holes? A faunal review. J. Zool. 295, 159–169.
- Zawierucha, K., Ostrowska, M., Vonnahme, T.R., Devetter, M., Nawrot, A.P., Lehmann, S., Kolicka, M., 2016a. Diversity and distribution of Tardigrada in Arctic cryoconite holes. J. Limnol. 75, 545–559.
- Zawierucha, K., Vonnahme, T.R., Devetter, M., Kolicka, M., Ostrowska, M., Chmielewski, S., Kosicki, J.Z., 2016b. Area, depth and elevation of cryoconite holes in the Arctic do not influence Tardigrada densities. Polish Polar Research 37, 325–334.
- Zawierucha, K., Buda, J., Pietryka, M., Richter, D., Łokas, E., Lehmann-Konera, S., Makowska, N., Bogdziewicz, M., 2018. Snapshot of micro-animals and associated biotic and abiotic environmental variables on the edge of the south-west Greenland ice sheet. Limnology 19, 141–150.
- Zawierucha, K., Buda, J., Fontaneto, D., Ambrosini, R., Franzetti, A., Wierzoń, M., Bogdziewicz, M., 2019. Fine-scale spatial heterogeneity of invertebrates within cryoconite holes. Aquat. Ecol. 53, 179–190. <https://doi.org/10.1007/s10452-019-09681-9>.